



# First survey of the Passalidae (Coleoptera, Scarabaeoidea) species from Reserva Ecológica de Guapiaçu (REGUA), Cachoeiras de Macacu, RJ, Brazil

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**Abstract:** We present the details of a survey with species of passalid conducted in the Reserva Ecológica de Guapiaçu (Cachoeiras de Macacu, Rio de Janeiro State) together with illustrations for each species and an identification key. The study includes material collected between May 2010 and October 2013. We identified 11 species in three genera and two tribes (Passalini and Proculini). Passalini comprised two genera, *Passalus* with six species, and *Spasalus* with one species, representing 71.42% of all the species encountered. Proculini was represented by only one genus *Veturius*, with four species, representing 28.57% of the species surveyed. Nine species were recorded for the first time from Cachoeiras de Macacu municipality.

**Key words:** Atlantic Forest; bess beetles; distribution; diversity

## INTRODUCTION

The family Passalidae is included in the superfamily Scarabaeoidea and contains about 1,000 species in two tribes (Passalini and Proculini), of which at least 50% have been identified in America (Fonseca and Reyes-Castillo 2004; Boucher 2006; Mattos and Mermudes 2014). Passalidae is a morphologically homogeneous group. Species of this family live in decaying trunks and members of the colony show subsocial behavior, with complex acoustic communication between adults and larvae (Schuster 1983; Mattos and Mermudes 2014). Furthermore, these species play an important role as primary decomposers in tropical forests and can act as possible conservation bioindicators in priority areas (Schuster 1984; Schuster et al. 2000; Fonseca and Reyes-Castillo 2004). However, only few studies on the systematics of this family have been conducted in the Atlantic Forest biome, which could be because of the small number of researchers in Brazil (Santos-Silva

2000; Mattos and Mermudes 2013; Mattos and Mermudes 2014).

The Atlantic Forest biome has great endemic species richness and actually represents only 7.5% of the original area (Myers et al. 2000). Thus, studies that contribute to the knowledge of biodiversity in the Atlantic Forest biome are highly relevant for conservation and management strategies. This study presents an inventory of passalid diversity in the Atlantic Forest area within the Reserva Ecológica de Guapiaçu (REGUA), and to our knowledge, is the first study of coleopteran species in the reserve. Thus, we expand the knowledge of the diversity of Passalidae in one of the last remaining conserved areas of the Atlantic Forest in the municipality of Cachoeiras de Macacu.

## MATERIALS AND METHODS

### Study site

Reserva Ecológica de Guapiaçu (REGUA) is a nongovernmental organization that protects about 6,000 ha of the Atlantic Forest, in the municipality of Cachoeiras de Macacu (22°25'09.9" S, 042°46'13" W), Rio de Janeiro state, Brazil (Figure 1). The main objective of REGUA is to conserve the remaining forests in the Guapiaçu valley in southeastern Brazil, and more than 80% of the land is part of the Parque Estadual dos Três Picos (Pimentel and Olmos 2011).

### Data collection

Field collecting was conducted between May 2010 and October 2013 in the REGUA, and from all marked trails in the conservation unit. We considered the samples collected into cold (April to September) and hot (October to March) periods, totaling ten samples. The insects were collected manually after inspection of decaying fallen logs by using knives and axes. A four-member group conducted twice-daily sampling, 4 h each in the morning and afternoon. A sample set





**Figure 1.** Localization of study areas in the Reserva Ecológica de Guapiaçu (REGUA), Cachoeiras de Macacu, Rio de Janeiro, Brazil, modified from IBGE and INEA.

comprised three consecutive collection days, totaling 24 h per sample set. Illustrations were made using a Leica MZ7.5 stereomicroscope fitted with a drawing tube. The sampling effort was assessed by verifying the accumulation curve of the species constructed with the observed richness and number of specimens collected in the study area. Passalid richness was estimated by three nonparametric estimators: the estimated richness obtained by Chao I is a function of the ratio of the number of observed species represented by a single individual (singletons) and the number of observed species represented by two individuals (doubletons). The other estimator used was ICE, which is a coverage estimator that focuses on species found in  $\leq 10$  sampling units; and Jack I employed the number of species that occur only a single sample, as based on the incidence (Magurran 2004). The analyses were carried by EstimateS Win8.20, with (Colwell 2006). All specimens were deposited in the Collection José Alfredo Pinheiro Dutra of the Universidade Federal do Rio de Janeiro.

RESULTS

The passalids that we found mainly represent a subset of those known from the more extensively surveyed Atlantic Forest as reported by Fonseca and Reye-Castillo (2004) who listed the passalids from Brazil, and more recently Mattos and Mermudes (2014) who listed Brazilian passalids from a continental Island in Rio de Janeiro state (Ilha Grande). We found eleven species of passalids reported by these authors from other localities (Fonseca and Reye-Castillo 2004; Mattos and Mermudes 2014). In this study, we report eleven passalids species in three genera which belonged to two Neotropical tribes of the Passalinae (Table 1). The species accumulation curves were based on the three different estimators Chao I, Jack I and ICE reached an asymptote when all species have been observed to 10 samples. These results represent more than 85% of the richness estimate and is significant with the sampling effort applied (Figure 2).

The list of Passalids from REGUA is organized by tribe, genera and species with information of valid scientific name and catalog information of the species, material examined, elevation of the collected, and distribution of the species. An identification key to the species of Passalidae recorded from REGUA is given.

**Table 1.** Number of Passalidae species from the Rio de Janeiro (RJ) state and Reserva Ecológica de Guapiaçu (REGUA).

Tribe	Genus	Species in RJ	Species in REGUA
Proculini	<i>Popilius</i>	1	0
	<i>Veturius</i>	6	4
Passalini	<i>Paxillus</i>	2	0
	<i>Spasalus</i>	2	1
	<i>Passalus</i>	25	6
Total		36	11

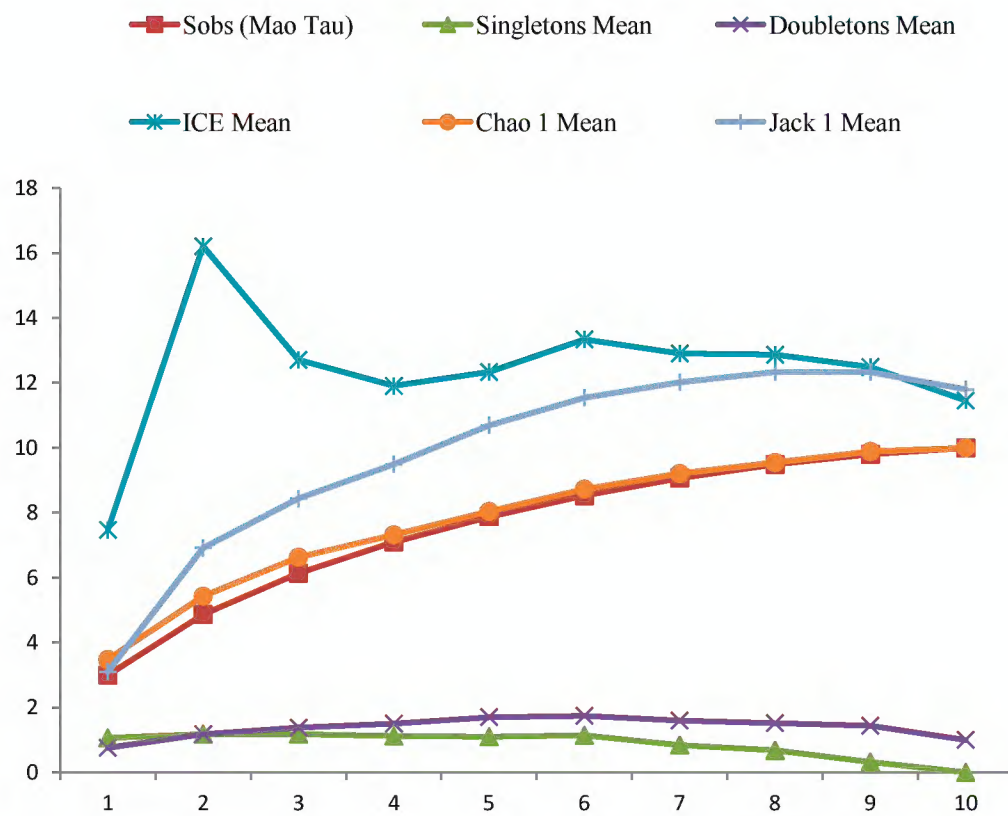
List of Passalidae from REGUA

***Passalus (Passalus) denticollis*** (Kaup, 1869), Figure 3  
*Phoroneus denticollis* Kaup, 1869: 11; Luederwaldt, 1931: 125  
*Passalus alius* Kuwert, 1891: 191; Luederwaldt, 1931: 138; Fonseca & Reyes-Castillo, 2004: 17 (cat.); Boucher, 2004: 109 (syn.)  
*Passalus (Mitrorhinus) denticollis*; Fonseca & Reyes-Castillo, 2004: 17 (cat.)  
*Passalus (Phoroneus) denticollis*; Boucher, 2004: 109

**Distribution:** Brazil: Bahia, Minas Gerais, Rio de Janeiro (Angra dos Reis, Ilha Grande), Cachoeiras de Macacu, Mendes, São Paulo, Santa Catarina, and Rio Grande do Sul.

**Material examined.** Brazil: *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, 1 specimen, 11.VII.2012, 60 m, Silveira col., I. Mattos det. 2012; Trilha Amarela, 3 specimens, 14.V.2011, 8 m, Mermudes et al. col., I. Mattos det. 2011; Trilha da Schincariol, 2 specimens, 14.V.2011, 47 m, Mermudes et al. col., I. Mattos det. 2011; Trilha da Cerca, 1 specimen, 20-23.V.2011, 35 m, Mermudes et al. col., I. Mattos det. 2011; Trilha Marrom, 1 specimen, 14.V.2011, 63 m, Mermudes et al. col., I. Mattos det. 2011; Trilha São





**Figure 2.** The accumulation curve of Passalidae species. Sobs: Total number of species observed in all samples. Singletons: single individual or case of rare species. Doubletons: two individuals or abundant species. See Supplemental Materials on-line.

José, 2 specimens, 10.XI.2012, 64 m, Mermudes et al. col., I. Mattos det. 2012; Trilha Amarela, 10, 30.VI.2013, 9 m, Mermudes & Mattos col., I. Mattos det. 2013; Trilha Verde, 1 specimen, 30.VI.2013, 230 m, Mermudes & Mattos col., I. Mattos det. 2013; Trilha Amarela, 3 specimens, 1.VI.2013, 10 m, Mermudes & Mattos col., I. Mattos det. 2013 (DZRJ).

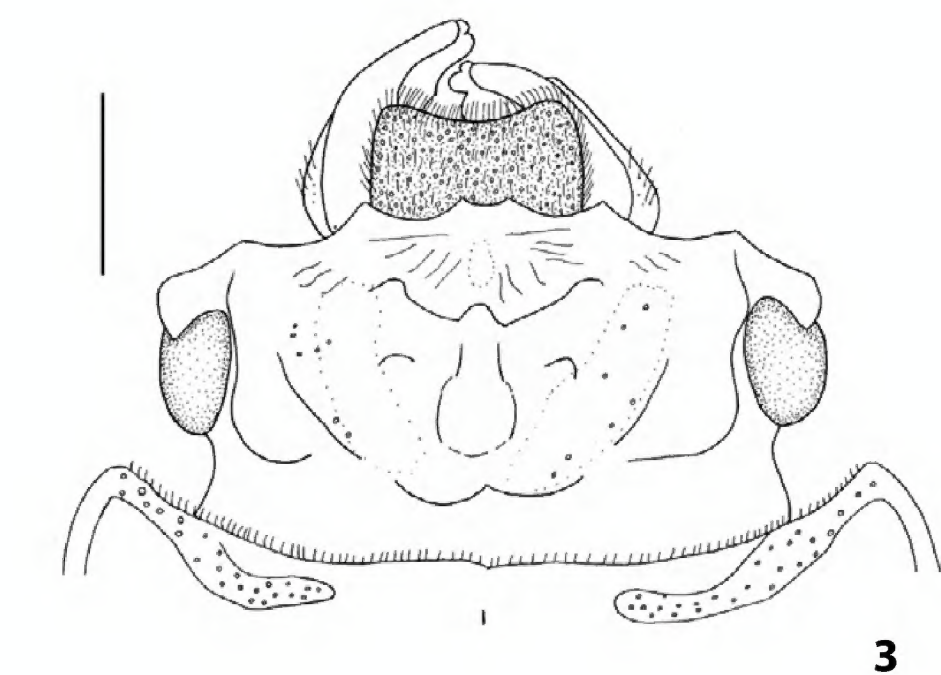
***Passalus (Passalus) glaberrimus* Eschscholtz, 1829,**

Figure 4

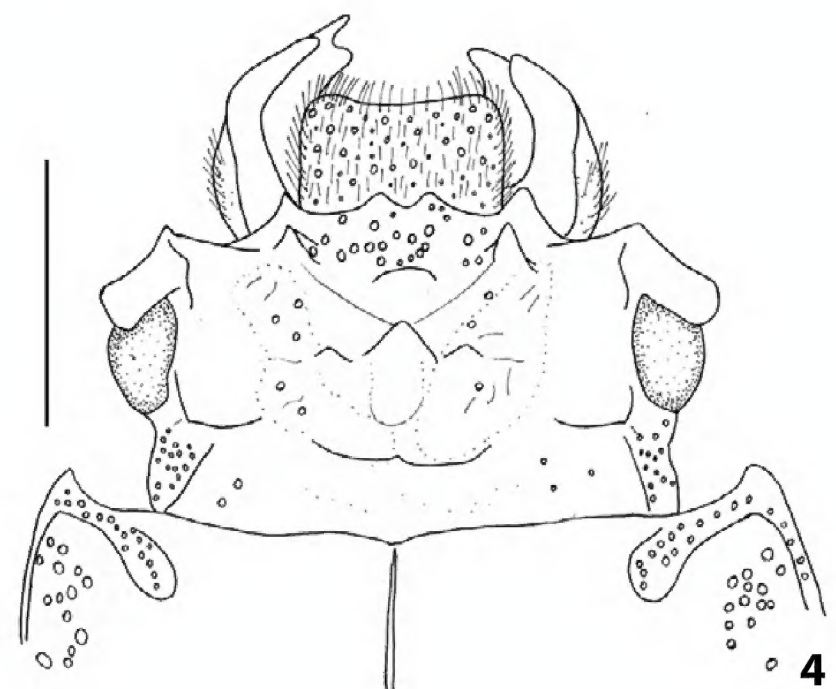
*Passalus (Passalus) glaberrimus* Eschscholtz, 1829: 20, Luederwaldt, 1931: 145; Fonseca & Reyes-Castillo, 2004: 17 (cat.).

**Distribution:** Guatemala, Brazil (Amazonas, Rio de Janeiro, São Paulo, Santa Catarina, and Rio Grande do Sul), and Argentina.

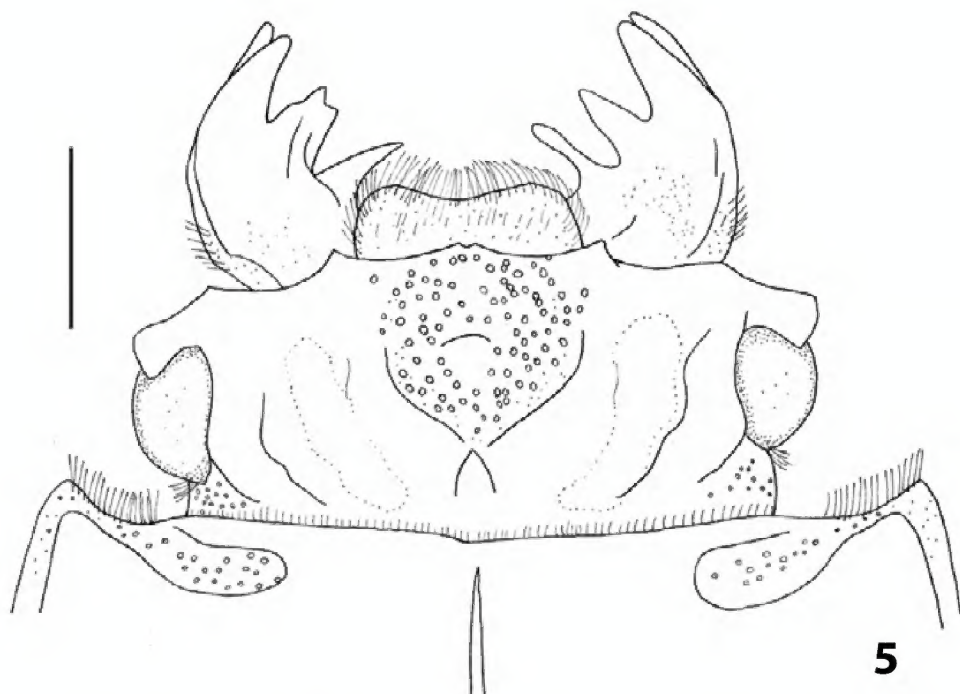
**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha da Pedra Dágua, 2 specimens, 20-23.V.2011, 200 m, Mermudes et al. col., I. Mattos det. 2011; Trilha Verde, 1 specimen, 11.XI.2012, 229 m, Mermudes et al. col., I. Mattos det. 2012 (DZRJ).



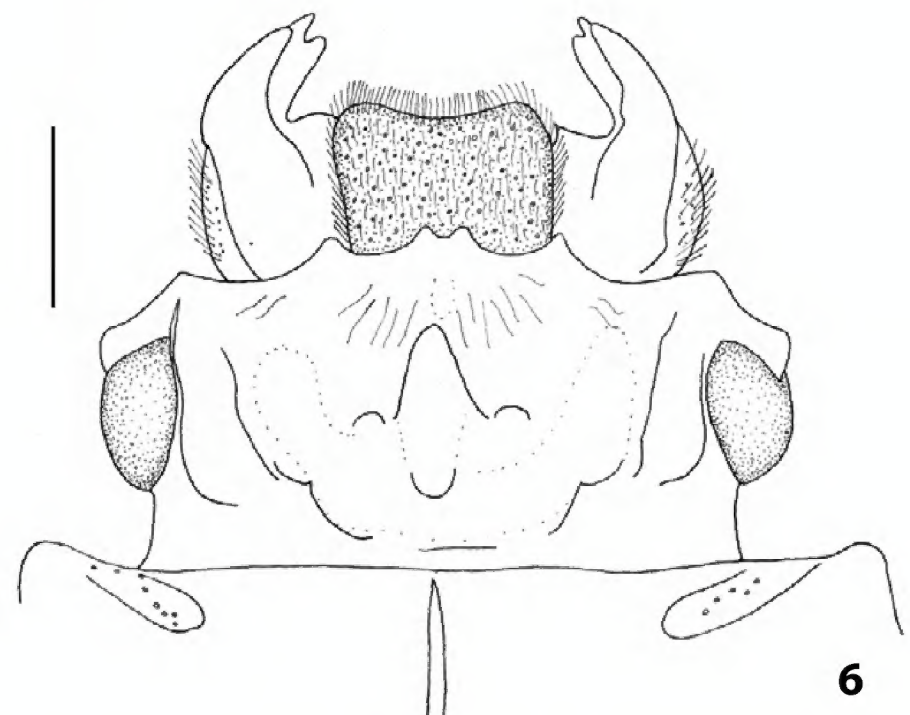
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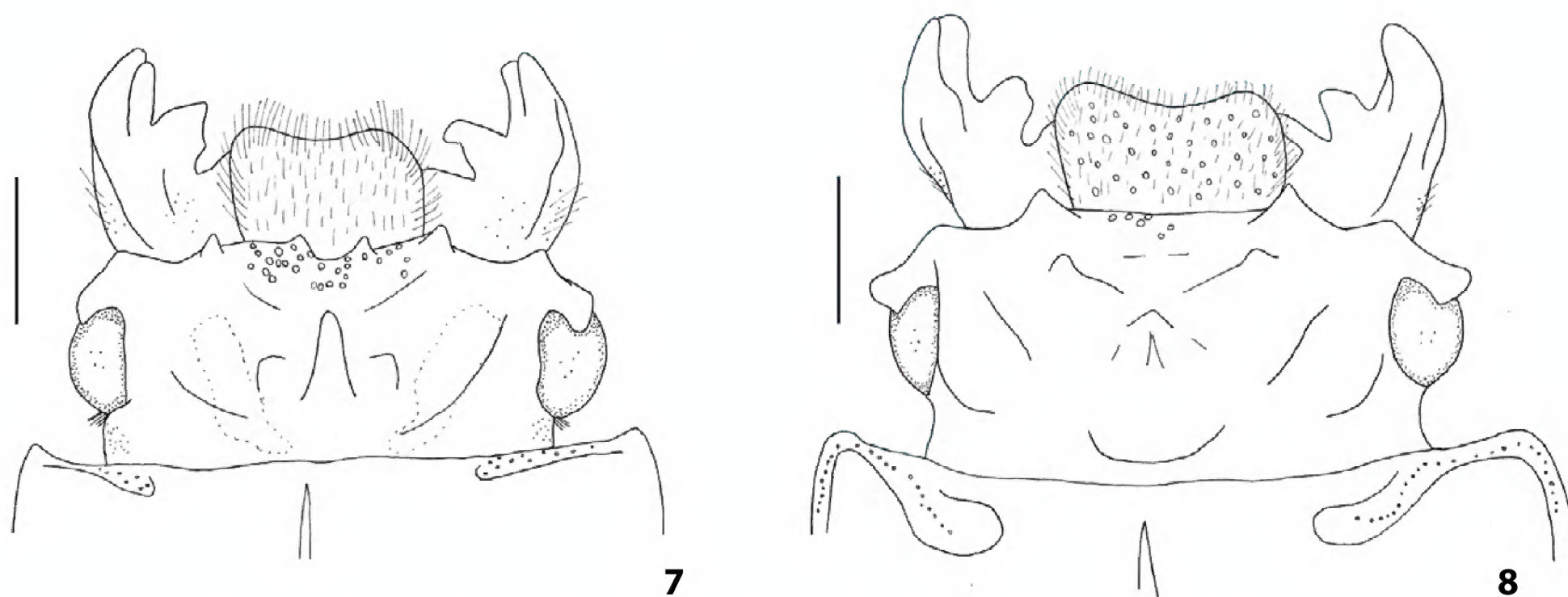
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**Figures 3–6.** Species of *Passalus*, Section Phoroneus, dorsal view of head: (3) *Passalus(Passalus) denticollis*; (4) *Passalus (Passalus) glaberrimus*; (5) *Passalus (Passalus) occipitalis*; (6) *Passalus (Passalus) quadricollis*. Scale bar = 1 mm.





**Figures 7–8.** Species of *Passalus*, dorsal view of head: (7) Section Neleus *Passalus* (*Passalus*) *punctiger*; (8) *Passalus* (*Pertinax*) *convexus*. Scale bar = 1 mm.

***Passalus* (*Passalus*) *occipitalis*** Eschscholtz, 1830,

Figure 5

*Passalus occipitalis* Eschscholtz, 1829: 21; Fonseca & Reyes-Castillo, 2004: 17 (cat.).

**Distribution:** Ecuador, Venezuela, Brazil (Goiás, Minas Gerais: municipalities of Lambari, and Caxambu, Rio de Janeiro: Ilha Grande, Itatiaia; São Paulo, Santa Catarina and Rio Grande do Sul), and Paraguay.

**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Fazenda Lengruber, Trilha do moinho, 2 specimens, 1.VI.2012, 280 m, Mermudes et al. col., I. Mattos det. 2012 (DZRJ).

***Passalus* (*Passalus*) *quadr collaris*** Eschscholtz, 1831,

Figure 6

*Passalus* (*Passalus*) *quadr collaris* Eschscholtz, 1829: 21; Fonseca & Reyes-Castillo, 2004: 18 (cat.).

**Distribution:** Brazil: Amazonas, Minas Gerais, Rio de Janeiro (Ilha Grande, Paraty, Itatiaia, Teresópolis, Petrópolis, Mendes), São Paulo, Santa Catarina, Rio Grande do Sul.

**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha Marrom, 10 specimens, 15.V.2011, 63 m, Mermudes et al. col., I. Mattos det. 2012 (DZRJ).

***Passalus* (*Passalus*) *punctiger*** Lepeletier & Serville, 1825, Figure 7

*Passalus punctiger* Lepeletier & Serville, 1825: 20; Fonseca & Reyes-Castillo, 2004: 20 (cat.).

**Distribution:** Mexico, Guatemala, Trinidad, Venezuela, Colombia, Guyana, French Guiana, Peru, Brazil (Amazonas, Rondônia, Pará, Amapá, Pernambuco, Goiás, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), and Paraguay.

**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, 2 specimens, 11.VII.2013, 60 m, Silveira col., I. Mattos det. 2013; 1

specimen, 11.VII.2013, 63 m, Mermudes & Mattos col., I. Mattos det. 2013; Trilha Amarela, 9 specimens, 8.VI.2012, 1 specimen, 10.XI.2012, 36 m, Mermudes et al. col., I. Mattos det. 2012; Trilha Marrom, 7 specimens, 28.VI.2013, 65 m, Mattos col. & det. 2013; Reserva Ecológica de Guapiaçu, Fazenda Lengruber, Trilha do moinho, 3 specimens, 1.VI.2013, 244 m, Mermudes et al. col., I. Mattos det. 2013 (DZRJ).

***Passalus* (*Pertinax*) *convexus*** Dalman, 1817, Figure 8

*Passalus* (*Pertinax*) *convexus* Dalman, 1817: 333; Luederwaldt, 1931: 114; Fonseca & Reyes-Castillo, 2004: 15 (cat.).

**Distribution:** Chile, Peru, Ecuador, Guiana and Brazil: Amazonas, Amapá, Acre, Pará, Rondônia, Roraima, Bahia, Rio de Janeiro, Minas Gerais, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul.

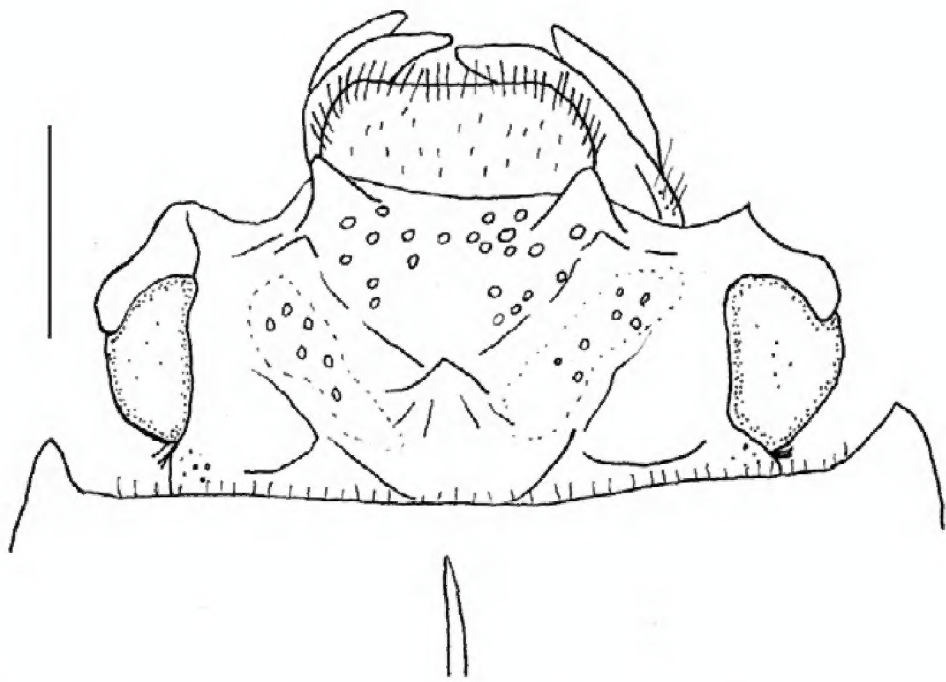
**Material examined.** Brazil. *Rio de Janeiro*: Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha Marrom, 15 specimens, 15.V.2011, 63 m, Mermudes et al. col., I. Mattos det. 2012, 3 specimens, 12.X.2013, 32 m, Trilha da Schincariol, 2 specimens, 14.V.2011, 47 m, Mermudes et al. col., I. Mattos det. 2012, Trilha São José, 13 specimens, 10.XI.2012, 163 m, Mermudes et al. col., I. Mattos det. 2012, Trilha Verde, 1 specimen, 11.XI.2012, 310 m, 3 specimens, 29.V.2013, 288 m, 7 specimens, 30.V.2013, 242 m, Mermudes et al. col., Trilha Cinza, 6 specimens, 30.V.2013, 319 m, Mermudes et al. col., Trilha Azul, 2 specimens, 31.V.2013, 209 m, Mermudes et al. col., Fazenda Lengruber, 2 specimens, 9.XI.2012, Mermudes et al. col., I. Mattos det. 2012, Trilha do moinho, 7 specimens, 1.VI.2013, 299 m, Mermudes et al. col. (DZRJ).

***Spasalus robustus*** (Percheron, 1835), Figure 9

*Spasalus robustus* Percheron, 1835: 35; Fonseca & Reyes-Castillo, 2004: 13 (cat.).

**Distribution:** Brazil (Goiás, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná Santa Catarina and





**Figure 9.** *Spasalus robustus*, dorsal view of head. Scale bar = 1 mm.

Rio Grande do Sul), Paraguay and Argentina.

**Material examined.** Brazil. *Rio de Janeiro*: Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha da Pedra D'água, 2 specimens, 20–23.V.2011, Trilha da Schincariol, 1 specimen, 14.V.2011, Mermudes et al. col., I. Mattos det. 2012 (DZRJ).

***Veturius (Veturius) sinuatus*** (Eschscholtz, 1829),

Figure 10

*Veturius (Veturius) sinuatus* Eschscholtz, 1829: 455; Boucher, 2006: 448.

**Distribution:** Brazil: Mato Grosso, Mato Grosso do Sul, Bahia, Goiás, Espírito Santo, Minas Gerais, Rio de Janeiro (Ilha Grande, Piabetá, Cachoeiras de Macacu), São Paulo (Ilha de São Sebastião), Paraná, Santa Catarina, Rio Grande do Sul. Guiana, Suriname, Paraguay and Argentina (Boucher 2006).

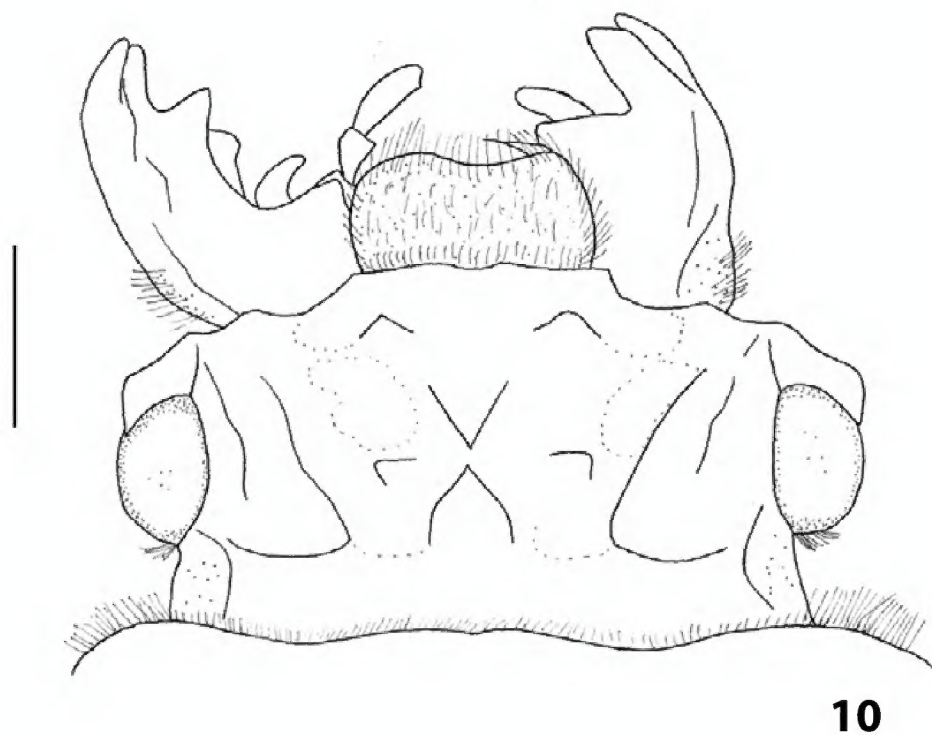
**Material examined.** Brazil. *Rio de Janeiro*: Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, 2 specimens, 27.X.2012, 63 m Mermudes et al. col. (DZRJ).

***Veturius (Veturius) simillimus*** Kuwert, 1891, Figure 11

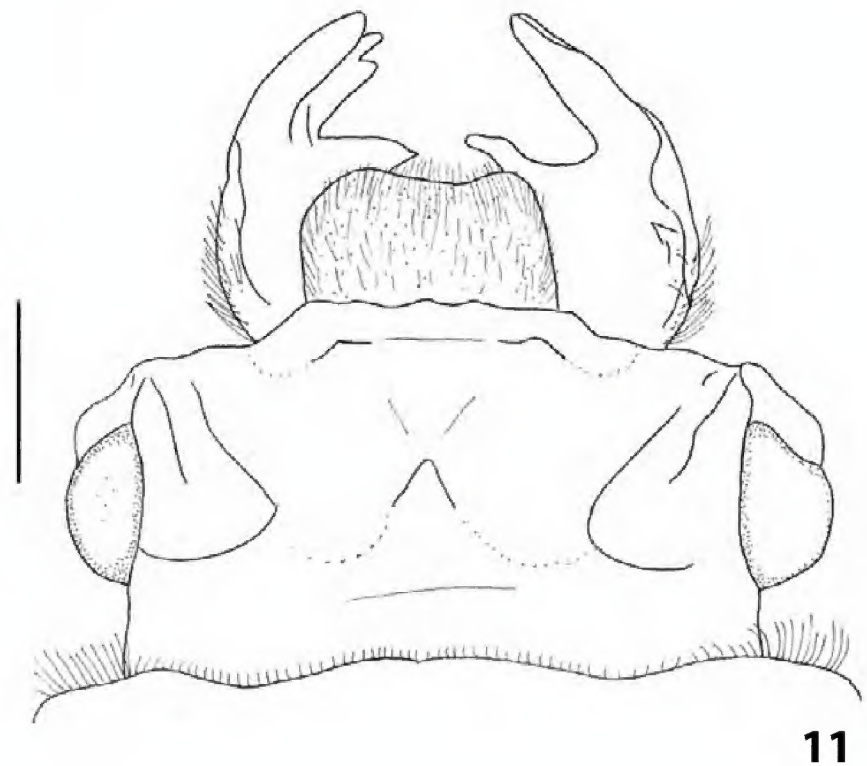
*Veturius (Veturius) simillimus* Kuwert, 1891: 493; Boucher, 2006: 493

**Distribution:** Species recorded only from Brazil: Minas Gerais, Espírito Santo, Rio de Janeiro (Ilha Grande, Casimiro de Abreu, Cachoeiras de Macacu), São Paulo, Paraná, and Santa Catarina.

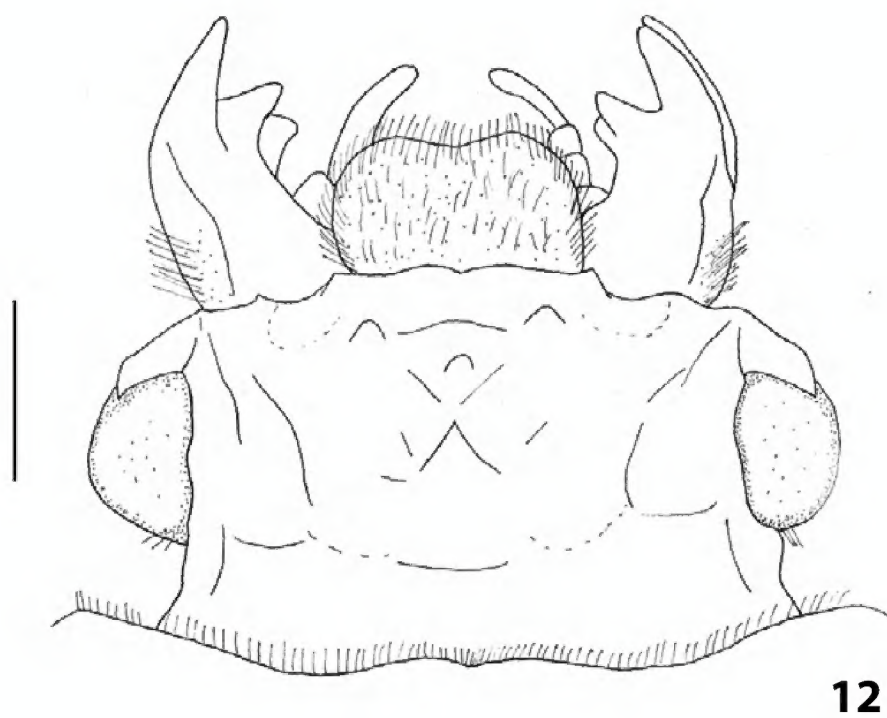
**Material examined.** Brazil. *Rio de Janeiro*: Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha Verde, 1 specimen, 28.XI.2013, 136 m, Mermudes et



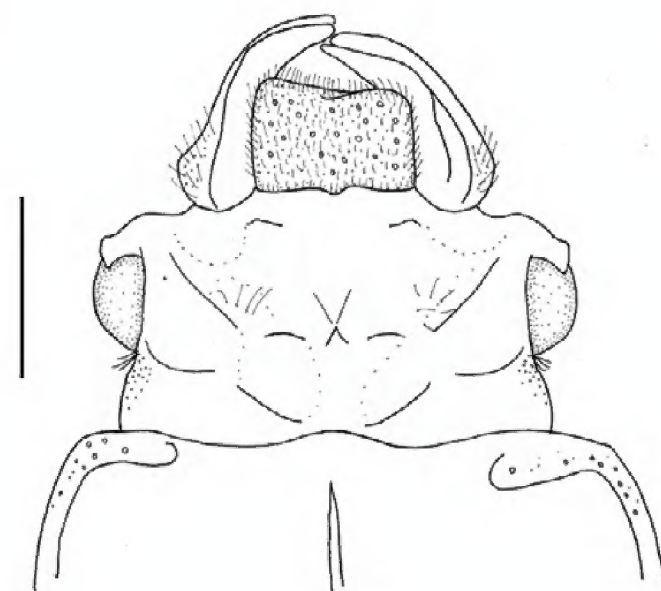
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**Figures 10–13.** Species of *Veturius*, dorsal view of head: (10) *Veturius (Veturius) sinuatus*; (11) *Veturius (Veturius) simillimus*; (12) *Veturius (Veturius) trans-verses*; (13) *Veturius (Veturius) assimillis*. Scale bar = 1 mm.



al. col, Trilha Marrom, 2 specimens, 15.V.2011, 70 m, Mermudes et al. col, Fazenda Lengruher, Trilha do moinho, 1 specimen, 28.XI.2013, 200 m, Mermudes et al. col. (DZRJ).

***Veturius (Veturius) transversus*** (Dalman, 1817),  
Figure 12

*Passalus transversus* Dalman, 1817: 143.

*Veturius (Veturius) transversus*; Boucher, 2006: 480.

**Distribution:** Brazil (Pernambuco, Bahia, Goiás, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Paraguay and Argentina.

**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Trilha verde, 2 specimens, 11.XI.2012, 306 m, Mermudes et al. col, Trilha cinza; 1 specimen, 30.V.2013, 320 m, Mermudes et al. col. (DZRJ).

***Veturius (Veturius) assimillis*** Weber, 1801, Figure 13  
*Veturius (Veturius) assimillis* Weber, 1801: 81; Boucher, 2006: 497.

**Distribution:** Brazil: Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo (Ilha de São Sebastião), Paraná, Santa Catarina, Rio Grande do Sul. Paraguay and Argentina

**Material examined.** Brazil. *Rio de Janeiro*, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, Fazenda Lengruher, Trilha do moinho, 1 specimen, 9.XI.2012, 310 m, Mermudes et al. col, Trilha Verde, 1 specimen, 11.XI.2012, 310 m, Mermudes et al. col, Trilha Cinza, 1 specimen, 30.V.2013, 347 m, Mermudes et al. col. (DZRJ).

**Identification key to the species of Passalidae from REGUA**

- 1a Clypeus hidden below the frontal area, never visible dorsally, with lateral clypeal fossae sharp, located on each side of the medial frontal tubercles. Anterior margin of pronotum straight, pronotal groove deep and wide to the sides, lacking lateral frontal fossae. Tribe Passalini .....2
- 1b Clypeus visible dorsally, separated the frontal area by frontal clypeal suture, without lateral clypeal fossae. Anterior margin of pronotum bilobate, pronotal groove deep and wide to the sides, with lateral frontal fossae. Tribe Proculini. *Veturius (Veturius)* Kaup. .... 8
- 2a Antennae always with five lamellae in club. Maxilla with lacinia unidentate in apical third. Prosternal process rhomboidal with truncate apex. Profemur with marginal groove in anterior margin in ventral view. *Spasalus* Kaup. Figure 9.  
..... *Spasalus robustus* Percheron, 1835
- 2b Antennae with three lamellae in club. Maxilla with lacinia bidentate in apical third. Prosternal process rhomboidal with thin apex. Profemur without

- marginal groove in anterior margin in ventral view. *Passalus* Fabricius. .... 3
- 3a Anterior margin of head usually straight, secondary median frontal tubercles absent. Pronotum with dense lateral pubescence. Subgenus *Pertinax*. Figure 8. .... *Passalus (Pertinax) convexus* Dalman, 1817
- 3b Anterior margin of head not straight, with 1 or 2 secondary median frontal tubercles. Pronotum usually glabrous or with scarce lateral pubescence. Subgenus *Passalus*. .... 4
- 4a Anterior margin of head with two secondary median frontal tubercles more or less separated. Anterior frontal area punctate. Frontal ridges short. Section "Neleus". Figure 7.  
..... *Passalus (Passalus) punctiger* LePeletier & Serville, 1825
- 4b Anterior margin of head with two secondary median frontal tubercles contiguous. Anterior frontal unpunctate. Frontal ridges long. Section "Phoroneus". ....5
- 5a Anterior frontal area not notched in the middle. Figure 4.  
..... *Passalus (Passalus) glaberrimus* Eschscholtz, 1829
- 5b Anterior frontal area notched in the middle. .... 6
- 6a Anterior and posterior frontal area densely punctate. Figure 5.  
..... *Passalus (Passalus) occipitalis* Eschscholtz, 1829
- 6b Anterior frontal area unpunctate, or with scarce punctuation. ....7
- 7a Central tubercle flattened dorsally and, in lateral view anvilshaped. Figure 6.  
... *Passalus (Passalus) quadricollis* Eschscholtz, 1829
- 7b Central tubercle with slight lateral expansion seen dorsally and in lateral view with a slight silhouette. Figure 3.  
..... *Passalus (Passalus) denticollis* Percheron, 1835
- 8a Mandibles with bifid apex. Figure 12.  
..... *Veturius (Veturius) transversus* Dalman, 1817
- 8b Mandibles with triple apex. ....9
- 9a Margin of pronotum fossae narrow. Meso and metatibiae without spine. Figure 11.  
..... *Veturius (Veturius) simillimus* Kuwert, 1891
- 9b Margin of pronotum fossae deep and wide to very wide. Meso and metatibiae with spine..... 11
- 10a Lateral post frontal area setigerous. Apical groove of sternite VII absent. Figure 13.  
..... *Veturius (Veturius) assimillis* Weber, 1801
- 10b Lateral post frontal area glabrous. Apical groove of sternite VII present. Figure 9.  
..... *Veturius (Veturius) sinuatus* Eschscholtz, 1829

**DISCUSSION**

Currently, there are 36 known species from Rio de Janeiro state, where over 70% is represented by *Passalus* and 15% by *Veturius* (Mattos and Mermudes 2014). A total of 169 adults of 11 species belonging to two tribes



of Passalinae were collected. To our knowledge, this represents the first record of passalid species in the Atlantic Forest area within the REGUA, representing 28% of the total passalid diversity in Rio de Janeiro (Table 1). The genus *Passalus* showed the highest diversity (60%), with 155 individuals collected, reflecting the great diversity of this genus in the Atlantic Forest as reported by Mattos and Mermudes (2014). In accordance with the nonparametric estimators of species richness, the first survey of Passalidae in the REGUA presented a strong tendency of exhaustive sampling, and with a completeness between 85 and 100%.

The main trails of the study site were all sampled, and the richness of passalids observed corresponded with the richness predicted by all three estimators used. Compared to other studies on Passalidae in tropical forests (Jiménez-Ferbans et al. 2010) the present study is as well sampled.

The survey of this work was conducted at the same altitude as our similar study at Ilha Grande (Mattos and Mermudes 2014). This species richness probably is due to the similarity of habitats and altitude on lowlands of Atlantic Forest, and also the geographic proximity between this two reserves (distant about 230 km).

The diversity of Passalidae in the REGUA comprises nine species in common with the fauna of Ilha Grande: *Passalus* (*Passalus*) *denticollis*, *P.* (*Passalus*) *occipitalis*, *P.* (*Passalus*) *quadricollis*, *P.* (*Passalus*) *punctiger*, *P.* (*Pertinax*) *convexus*, *Spasalus robustus*, *Veturius* (*Veturius*) *sinuatus*, *V.* (*Veturius*) *simillimus*, and *V.* (*Veturius*) *transversus*. On the other hand, *P.* (*Passalus*) *glaberrimus* and *V.* (*Veturius*) *assimillis* were only recorded in the REGUA, which is probably due to the presence of primary forest remnants in the unit conservation (Rocha et al. 2007).

The low dispersal abilities, which are dependent on intraspecific adult and larval interactions, make passalids very sensitive to the disappearance of native forests. Moreover, temperature and specific vegetation requirements may be an important factor in distribution of endemic species of passalids. Thus, passalids may be much less resilient than other groups of indicator insects such as butterflies, ants and dung beetles (MacVean and Schuster 1981; Schuster et al. 2000; Schuster and Cano 2006; Jackson et al. 2009).

## SUPPLEMENTARY MATERIAL

Raw data for Figure 2, the accumulation curve of Passalidae species is available on-line:

- raw\_data\_Figure\_2.xls, 36 KB, MS Excel

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